

Quantifying the effect of viewpoint changes on sensitivity to face identity

Swystun, Alexander G.; Logan, Andrew J.

Published in:
Vision Research

DOI:
[10.1016/j.visres.2019.09.006](https://doi.org/10.1016/j.visres.2019.09.006)

Publication date:
2019

Document Version
Author accepted manuscript

[Link to publication in ResearchOnline](#)

Citation for published version (Harvard):
Swystun, AG & Logan, AJ 2019, 'Quantifying the effect of viewpoint changes on sensitivity to face identity', *Vision Research*, vol. 165, pp. 1-12. <https://doi.org/10.1016/j.visres.2019.09.006>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

If you believe that this document breaches copyright please view our takedown policy at <https://edshare.gcu.ac.uk/id/eprint/5179> for details of how to contact us.

Quantifying the effect of viewpoint changes on sensitivity to face identity

Alexander G Swystun^a and Andrew J Logan^{a,b*}

^a School of Optometry and Vision Science, University of Bradford, UK.

^b Department of Vision Sciences, Glasgow Caledonian University, UK.

* Corresponding author

Correspondence:

Alexander G Swystun A.G.Swystun@student.bradford.ac.uk

Andrew J Logan; Andrew.Logan@gcu.ac.uk

Abstract

Although faces can be recognized from different viewpoints, variations in viewpoint impair face identification ability. The present study quantified the effect of changes in viewpoint on sensitivity to face identity. We measured discrimination thresholds for synthetic faces presented from several viewpoints (same viewpoint condition) and the same faces shown with a change in viewpoint (5° , 10° or 20°) between viewing and test. We investigated three types of viewpoint change: (i) front-to-side (front-view matched to 20° side-view), (ii) side-to-front (20° side-view matched to front) and (iii) symmetrical (10° left to 10° right). In the same viewpoint condition, discrimination thresholds were lowest for faces presented from 0° and increased linearly as the viewing angle was increased (threshold elevations: $0^\circ = 1.00\times$, $5^\circ = 1.11\times$, $10^\circ = 1.22\times$, $20^\circ = 1.69\times$). Changes in viewpoint between viewing and test led to further reductions in discrimination sensitivity, which depended upon the magnitude of viewpoint change ($5^\circ = 1.38\times$, $10^\circ = 1.75\times$, $20^\circ = 2.07\times$). Sensitivity also depended upon the type of viewpoint change: while a 20° front-to-side viewpoint change increased discrimination thresholds by a factor of $2.09\times$, a symmetrical change in viewpoint, of the same magnitude, did not significantly reduce sensitivity ($1.26\times$). Sensitivity to face identity is significantly reduced by changes in viewpoint. Factors which determine the extent of this reduction include the magnitude of viewpoint change and symmetry. Our results support the premise of viewpoint-dependent encoding of unfamiliar face identities, and suggest that symmetry may be used to recognize identities across different viewpoints.

Keywords: face perception, viewpoint, psychophysics, unfamiliar faces.

1. Introduction

Faces are among the most complex objects processed by the visual system and contain a wealth of information. A brief glimpse of a face can reveal information about an individual's age, gender, ethnicity, emotional state and direction of attention. Importantly, faces also enable the visual system to recognize individual identities.

Recognition of face identity is robust to changes which transform the retinal input to the visual system. For example, transitioning from a smile to a frown modifies the position and shape of individual features. Nevertheless, although processing of facial identity and expression may interact (Lander and Butcher, 2015), familiar faces can still be identified, despite changes in facial expression (Schweinberger & Soukup, 1998). Similarly, large changes in face size have no effect on the ability to discriminate between unfamiliar face identities (Lee, Matsumiya & Wilson, 2006).

Faces are encountered from a range of different viewpoints. Although changes in viewpoint transform the information provided to the visual system, humans can recognize identities across different viewing angles (Hill, Schyns & Akamatsu, 1997; Lee et al., 2006; Newell, Chiroro & Valentine, 1999).

1.1. Encoding of face viewpoint

The strategies which enable the visual system to recognize faces across different viewpoints have yet to be fully elucidated (Ramírez, 2018). Neurophysiological evidence suggests that the majority of face-selective neurons within the temporal lobe of the macaque brain are tuned to specific viewpoints (Desimone, Albright, Gross et al., 1984; Freiwald & Tsao, 2010; Perrett, Oram, Harries et al., 1991; Perrett, Smith, Potter et al., 1985; Tanaka, Saito, Fukada et al., 1991). For example, Perrett et al. (1991) reported that, in general, activation of head-selective cells was maximal for one viewpoint, and declined monotonically as the face was rotated in either direction. Tuning for face viewpoint varies across neuronal populations; while some cells respond maximally to front-views, others are tuned to side or profile views (Desimone et al., 1984; Perrett et al., 1991). It has been proposed that encoding of activity across a population of neurons, with different viewpoint preferences, is required to recognize identities across changes in viewpoint (Perrett, Mistlin & Chitty, 1987; Perrett, Hietanen, Oram et al., 1992).

In humans, fMRI studies point to the conclusion that representations of unfamiliar faces within the fusiform face area (FFA) are also viewpoint-dependent. Specifically, repeated presentation of an unfamiliar identity from the same viewpoint is associated with a significant reduction in the BOLD signal recorded from the FFA (Andrews & Ewbank, 2004; Grill-Spector, Kushnir, Edelman et al., 1999; Xu, Yue, Lescroart et al., 2009). Presentation of the same identity from a

different viewpoint, however, releases this adaptation. These results suggest that different viewpoints of unfamiliar faces are encoded by dissociable populations of neurons.

More recently, it has become clear that symmetry plays a key role in the encoding of face identity across different viewpoints. For clarity, throughout this article, we use symmetry to refer to symmetrical changes in viewpoint around the frontal axis (e.g. 10° right to 10° left), unless otherwise specified. While the majority of face-selective neurons within the macaque brain are unimodally tuned to a single viewpoint, a number respond strongly to both a specific viewpoint (e.g. 45° right), and its symmetrical counterpart (45° left), but not intervening viewpoints (De Souza, Eifuku, Tamura et al., 2005; Freiwald & Tsao, 2010). This gives rise to a bimodal tuning pattern for certain viewpoint-selective neurons: one peak of cell activity for a specific viewing angle, and a second peak for the symmetrical viewpoint (Logothetis & Sheinberg, 1996; Perrett et al., 1991). Similarly, in humans, fMRI (Axelrod & Yovel, 2012; Kietzmann, Swisher, König et al., 2012) and ERP (Kietzmann, Gert, Tong et al., 2017) studies have reported evidence of symmetrical encoding of face viewpoint within brain regions which have been implicated in face processing.

1.2. Viewpoint-dependent face identification

Behavioral studies also point to the conclusion that face identification is viewpoint-dependent. Changes in viewpoint are associated with a reduction in both the accuracy (Hill et al., 1997; O'toole, Edelman & Bülthoff, 1998) and speed (Bruce, 1982; Newell et al., 1999) of face identification. The majority of these studies focused upon recognition of familiar, or learned, faces (Bruce, 1982; Hill et al., 1997; O'toole et al., 1998). As a result, the detrimental effect of viewpoint changes could be explained by difficulty matching faces across viewpoints to representations stored within memory.

Viewpoint changes, however, also impair the ability to discriminate between novel, unfamiliar face identities (Favelle, Hill & Claes, 2017; Guy, Habak, Wilson et al., 2017; Habak, Wilkinson & Wilson, 2008; Lee et al., 2006; Meinhardt-Injac, Meinhardt & Schwaninger, 2009; Morin, Guy, Habak et al., 2015; Newell et al., 1999; Troje & Bülthoff, 1996; Wilson, Loffler & Wilkinson, 2002). The paradigms employed by these studies made minimal memory demands. Accordingly, it seems that changes in viewpoint impair perceptual sensitivity to face identity, independently of memory. For example, Lee et al. (2006) found that the ability to match two face identities declined as the discrepancy between their viewpoints was increased.

Currently, there is limited evidence about the factors which determine the cost of viewpoint change on the ability to discriminate between face identities. It has been suggested that larger viewpoint changes are associated with poorer face discrimination performance (Lee et al., 2006). A number of previous studies utilized wide angular changes in face viewpoint, such as

three-quarter (45°) and profile (90°) views (Bruce, 1982; Bruce, Valentine & Baddeley, 1987; Hill et al., 1997; Nordt & Weigelt, 2017). Face rotations of this magnitude, however, occlude cardinal face features, such as the eyes and mouth (McKone, 2008). Accordingly, the decrease in discrimination ability associated with these viewpoint changes could be partly explained by reductions in the available information. Favelle, Palmisano and Avery (2011), on the other hand, measured the impact of a range of changes in viewpoint (15°, 30°, 45°, 60° and 75°) on face identification accuracy. While the authors reported that, overall, performance depended upon the magnitude of viewpoint change, it remains unclear if small (<30°) variations in viewpoint are sufficient to impair identification ability, relative to when faces were presented from the same viewing angle. The nature of the relationship between magnitude of viewpoint change and sensitivity to face identity also remains to be quantified.

The present study focused upon a comparatively narrow band (frontal $\pm 20^\circ$) of viewpoints which ensured that all features remained visible. We systematically compared discrimination sensitivity for faces presented from a range of near-frontal viewpoints (0°, 5°, 10°, 20°) in order to determine the robustness of the visual system to small variations in face viewpoint within the range which may be encountered in the natural environment.

Other lines of evidence suggest that the reduction in face discrimination ability depends on factors other than magnitude of viewpoint change. For example, there are significant differences in identification accuracy for different viewpoints. Specifically, frontal (Lee et al., 2006; Nordt & Weigelt, 2017) and three-quarter viewpoints (Bruce et al., 1987; O'toole et al., 1998) may offer an identification advantage over other viewing angles. Evidence for the latter, however, is mixed: Liu and Chaudhuri (2002) found limited support for superior recognition of faces presented from a three-quarter viewpoint. As outlined above, neuroimaging evidence suggests that the human visual system demonstrates specific sensitivity to faces presented from symmetrical viewpoints (Axelrod & Yovel, 2012; Kietzmann et al., 2012). For example, using fMRI, Kietzmann and colleagues reported that there was a greater degree of similarity between brain patterns for faces presented from mirror-symmetrical viewpoints (e.g. 10° left to 10° right), relative to asymmetrical viewpoints (frontal view to 20° right). Finally, it has been reported that the effects of viewpoint change on sensitivity to face information depends upon the face features which are manipulated (Meinhardt-Injac et al., 2009).

The present study empirically determined the cost of a variety of changes in viewpoint on sensitivity to face identity. We systematically varied the magnitude, direction and symmetry of viewpoint changes in order to quantify the effects of these factors on face discrimination ability.

Many previous studies investigated the effect of variations in viewpoint on face perception ability by measuring the accuracy with which participants make judgements about the identity of face images selected from a database (e.g. Favelle et al. 2011; Troje and Bühlhoff, 1996;

Van der Linde & Watson, 2010). Since this approach offers limited control of the perceptual difference between individual faces (i.e. perceived similarity), manipulation of an alternative parameter is needed to control task difficulty (e.g. Troje and Bühlhoff (1996) varied presentation time to achieve a specific error rate).

Our approach is based on synthetic faces: simplified stimuli which capture the major geometrical information (head-shape, hairline, feature size and position) of a face photograph, but exclude other details, such as hair color and skin texture (Wilson et al., 2002). In addition to being simplified, synthetic faces have the advantage that they can be manipulated in a controlled and precise way. This enabled us to directly quantify sensitivity to face identity by using a match-to-sample discrimination task to measure a discrimination threshold for faces presented from different viewpoints. The face discrimination threshold represents the minimum geometrical difference required between faces for accurate discrimination.

2. Methods

2.1. Synthetic faces

The complexity of faces can make it difficult to attribute differences in perceptual sensitivity to specific aspects of face information.

Synthetic faces were created by digitizing the salient geometrical face information from grayscale face photographs with neutral expressions (figure 1-top) (Wilson et al., 2002). Some details from this section are reproduced from Logan, Gordon & Loffler, 2017. Firstly, a polar coordinate grid was superimposed on the face photograph, centered on the bridge of the subject's nose. The external head-shape was sampled at 16 locations, angularly positioned at equal intervals of 22.5° . The positions of these points were used to define 7 radial frequencies (RFs) that describe the subject's head-shape. Radial frequency patterns are closed contours (Wilkinson, Wilson & Habak, 1998) that can be combined to capture the shape of objects such as animal torsos, fruit (Wilson & Wilkinson, 2002) and heads (Wilson et al., 2002). A further 9 points were utilized in the same way to define the shape of the subject's hairline.

The internal face features were sampled by 14 additional measurements. All internal features carried positional information (derived from the photograph), relative to the center of the face and the other features. The mouth and nose also carried shape information. Mouth and nose shapes were produced by altering generic feature templates in terms of length and width based on individual face measurements from the original face photographs. Eyes and eyebrows were generic in shape but provided additional positional information that was independent of the other features because they were presented in pairs.

In sum, each synthetic face is defined by 37 parameters and represented by a 37-dimensional vector (see (Wilson et al., 2002) for further details).

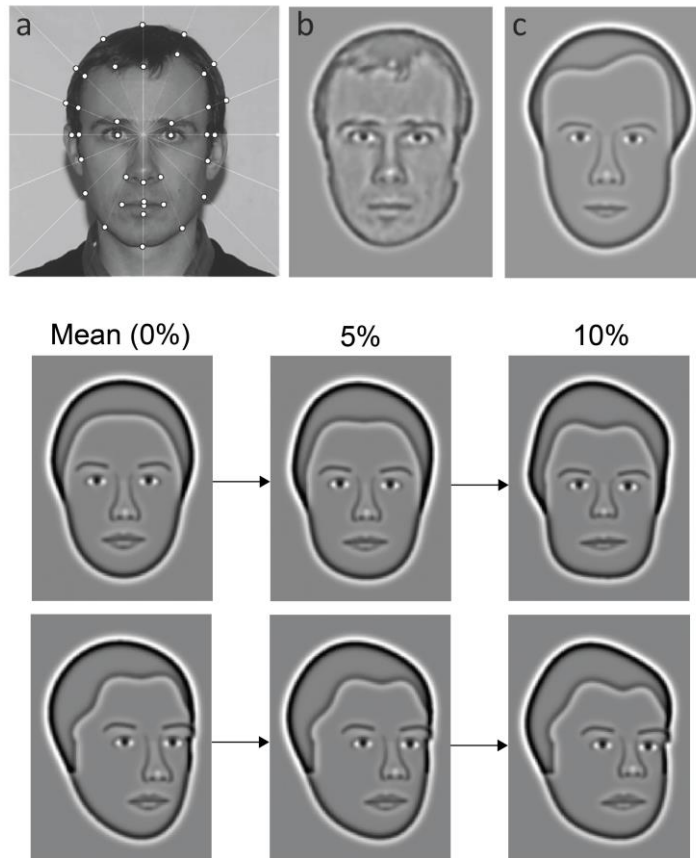


Figure 1. Synthetic faces. Top: (a) Grayscale photograph superimposed with a polar coordinate grid centered on the bridge of the nose. The head-shape was measured at 16 locations around the external contour, angularly positioned at equal intervals of 22.5° (outermost small white circles), 9 points in the upper half of the face captured hairline information. The positions and shapes of the internal face features were defined by 14 additional measurements. The position of all features was idiosyncratic, as derived from the photograph. The shapes of the eyes and eyebrows were generic; those of the mouth and nose were individualized. In sum, each synthetic face is defined by 37 parameters and represented by a 37-dimensional vector (see (Wilson et al., 2002) for further details). (b) Photograph filtered with a 2.0 octave bandwidth DOG filter with peak spatial frequency of 10 c/face width. (c) Corresponding synthetic face. This procedure was then repeated using grayscale photographs with the subject facing 20° to the side in order to create synthetic faces depicted from the 20° side viewpoint. Bottom: Face morphing. Synthetic faces were adjusted by manipulating their distinctiveness, i.e. by how much they differ from the mean face (left). Increasing face distinctiveness results in individual faces becoming progressively more dissimilar (from middle to right) to the mean face, in the direction of a specific identity. The upper and lower rows illustrate the effect of increasing distinctiveness for the same face identity

presented from the frontal and 20° side views respectively. Distinctiveness is expressed as a percentage of the mean head radius and quantifies the total geometric variation between the specified face and the mean face. Typical observers can discriminate a face identity from the mean at about 5% distinctiveness (Wilson et al., 2002).

In addition to the frontal viewpoint, face photographs were also taken with the subject facing 20° to the right side. The process outlined above was then applied to these images to create synthetic faces for the same identities depicted from a 20° side view. Each identity was therefore represented by both a frontal and 20° right side view synthetic face (figure 1-bottom). Left views of the same synthetic faces were created by mirror-symmetric transformation of the stimuli.

The parameters of these frontal and 20° side view synthetic faces were then combined to create depictions of the same identity from intervening viewpoints (see Lee et al., 2006 for a full description). For example, in order to create a synthetic face identity presented from a 10° side view, the parameters of the frontal and 20° side synthetic faces were combined with 50:50 weighting. A 5° side view, on the other hand, was created by disproportionate (75%) weighting of the front, relative to side (25%), view parameters. This transformation was applied to each of the 37 parameters which are used to describe each synthetic face.

Although simplified, synthetic faces contain sufficient information for accurate identification (Wilson et al., 2002). For example, while color (e.g. skin, hair and eye) and texture are present in real faces, faces can be identified without this information. Since they are intended to contain the minimum information required for identification, synthetic faces include neither color nor texture.

The face images were band-pass filtered at the spatial frequency which has been reported to be optimal for face identification (10 cycles/face width, circular difference of Gaussian filter with a bandwidth of 2.0 octaves) (Näsänen, 1999). While the optimal spatial frequency may be task-dependent, the resulting faces accentuate geometric information in the most important frequency band while omitting cues such as hair and skin texture, skin color and wrinkles. It should also be noted that synthetic faces only contain two-dimensional information.

All face measurements (i.e. the 37-dimensional vector representing each face) were normalized by the mean head size of the respective gender, resulting in faces that differed in terms of individual features (e.g. head-shape and eye position), but not overall size. A mean female face was produced by averaging each of the 37 parameters of all 40 female face

identities, shown from the same viewpoint. A mean face was produced for each of the frontal and 20° side viewpoints. Within this framework, synthetic faces can be manipulated to have a defined difference from the mean face (figure 1-bottom). This geometric difference quantifies the total difference of a face from the mean (i.e. its distinctiveness), expressed as a percentage of the mean head radius. It has been shown that this metric captures discrimination sensitivity, independently of face identity (Wilson et al., 2002).

Synthetic faces from four different Caucasian female individuals were used. At the test distance of 1.20m, each face subtended 5.5° of visual angle in height.

2.2. Observers

Six participants (including two authors) (mean age = 26.7 years old, range = 19-39) completed these experiments. All six participants (three male) were in good health with normal, or corrected-to-normal, vision (visual acuity 20/20 or better, no visual abnormalities). Participants gave informed consent in accordance with the Declaration of Helsinki, as approved by the Biomedical, Natural, Physical and Health Sciences Research Ethics Panel of the University of Bradford.

2.3. Apparatus

All trials were completed under binocular viewing, under an ambient illumination of 72 cd/m². Observers were seated at 1.20m from a computer monitor. Accurate viewing distance was maintained with a chin and forehead rest. Stimuli were created in Matlab (www.mathworks.com) and presented, using routines from the Psychtoolbox extension (Brainard, 1997; Kleiner, Brainard, Pelli, 2007; Pelli, 1997), on a Sony Trinitron G500 high resolution monitor (1024 X 768 at 85 Hz) of 61 cd/m² mean luminance which was controlled by a Mac mini computer. Equally spaced gray levels were used to maximize contrast linearity. At the test distance, the computer monitor subtended 18.6° by 14.7° of visual angle; one pixel was 0.018°.

2.4. Procedure

The same match-to-sample, two-alternative forced choice (2-AFC) procedure, using the method of constant stimuli, was utilized across all conditions (figure 2). A target face was shown for 250ms, followed by a low-level, Gaussian luminance mask for 200ms. The mask was created by applying the same band-pass filter used to create the synthetic faces to a two-dimensional binary noise array. The mask was used to remove any residual visual transient from the target exposure.

Following the offset of the mask, two comparison faces were presented side-by-side. One of them was the target (figure 2). To adjust task difficulty, the other (distractor) differed from the

target in terms of face distinctiveness (figure 1-bottom) by a specific amount, dependent upon observer sensitivity and condition. The observer was asked to indicate the target via keyboard press (left or right arrow). The two choices remained on the screen until the decision had been made. Participants were encouraged to respond quickly and guess when uncertain. No feedback was provided.

Discrimination thresholds were measured for three viewpoint conditions (see 2.4.1-2.4.3), presented randomly within an experimental block, using an interleaved design. Each condition was repeated for four different identities, intermixed in the interleaved design. Accordingly, observers were uncertain about (i) the face identity and (ii) type of viewpoint change being tested on each trial.

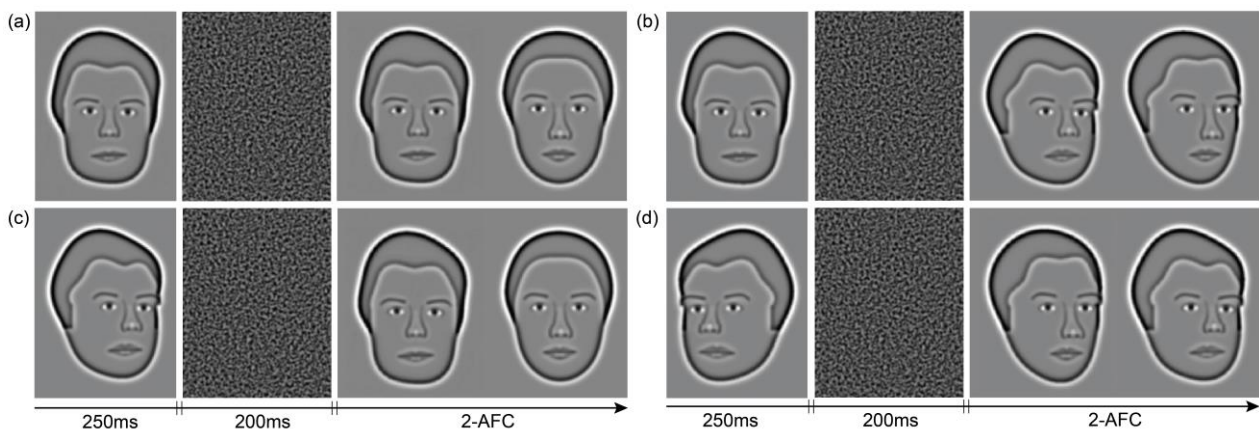


Figure 2. Procedure. The same procedure was utilized across all conditions. A target face was shown for 250ms, followed first by a mask (200ms), and then two comparison faces, side-by-side. Observers had to select which of the two faces matched the target (two-alternative forced choice, 2-AFC). (a) Same viewpoint condition. Target and comparison faces were presented from the same viewpoint. In this example, all faces were shown from the frontal (0°) viewpoint. A face (left-hand side in 2-AFC) with a distinctiveness of 10% was the target, which had to be discriminated from the mean face (0% distinctiveness; distractor). (b) Front-to-side viewpoint change condition. In this condition, observers had to match face identity across a change in viewpoint. While the target face was shown from the front, the comparison faces were presented from a side viewpoint (20° right in this example). (c) Side-to-front viewpoint change condition. This was similar to (b), but the order was reversed: while the comparison faces were shown from the front, the target face was presented from a side viewpoint. (d) Symmetrical viewpoint changes. A target face is presented from a side viewpoint (20° left in this example). The comparison faces are presented from the symmetrical viewpoint (20° right).

For each condition, discrimination accuracy for each identity was measured at 6 increments of face distinctiveness. The 6 increments were chosen to sample the range between 50-100% accuracy. The absolute increment values depended on the sensitivity of each observer and the difficulty of the discrimination task. The increments were selected on the basis of pilot experiments undertaken by each observer prior to data collection. Each level of distinctiveness was tested 20 times per identity, resulting in 120 trials for each determination of threshold. As a result, 480 trials (120 X 4 identities) were required for each viewpoint that was tested. Data were fit by a Quick function (Quick, 1974) using a maximum likelihood procedure (separately for each condition, and each identity). Discrimination thresholds were subsequently extracted from the fitted functions and defined as the distinctiveness value which was associated with 75% accuracy.

2.4.1. Condition 1: Same viewpoint

There was no viewpoint change in this condition; the target and comparison faces were all presented from the same viewpoint (figure 2a). Observers were required to discriminate between the mean face and a face which differed from the mean face by a specific level of face distinctiveness (figure 1-bottom). To determine if sensitivity to face identity depends upon viewpoint, discrimination thresholds were measured for four different viewpoints: frontal (0°), 5°, 10° and 20° (see icons in figure 3). To investigate the effect of direction, discrimination thresholds were measured independently for faces presented in both lateral directions (e.g. 10° left and 10° right). A target face (250ms) was presented from one of these four viewpoints, followed by the mask, and then two comparison faces (one target, the other distractor), shown from the same viewpoint as the target.

2.4.2. Condition 2: Front and side viewpoint changes

The procedure was the same as above; however, observers were now required to match face identities across changes in viewpoint. While the target face (250ms) was presented from the frontal viewpoint (0°), the two comparison faces were presented from one of three side viewpoints (5°, 10° and 20°) (front-to-side viewpoint change; figure 2b). As for condition 1, discrimination thresholds were measured in both lateral directions (e.g. frontal to 10° left and frontal to 10° right).

This condition was then repeated with the order of viewpoint presentation reversed: the target face (250ms) was presented from one of three side viewpoints (5°, 10° and 20°) while the two comparison faces were shown from the frontal view (0°) (side-to-front viewpoint change; figure 2c).

The same four face identities were used from condition 1. This enables direct comparison of sensitivities across any of the conditions tested in these experiments.

2.4.3. Condition 3: Symmetrical viewpoint changes

Symmetrical viewpoint changes were defined as rotations of face viewpoint, around the frontal axis, of equal magnitudes in each lateral direction (figure 2d). The target face (250ms) was presented from a specific side viewpoint (e.g. 10° left); the comparison faces were then shown from the symmetrical side viewpoint (10° right). Three magnitudes of symmetrical viewpoint changes were tested: 40° (20° left to 20° right), 20° (10° left to 10° right) and 10° (5° left to 5° right). To investigate the effect of viewpoint change direction, each condition was repeated in the opposite lateral direction (i.e. right to left).

2.5. Statistical analysis

All statistical analyses utilized a one-factor, repeated measures ANOVA, unless otherwise specified. Where Mauchly's test indicated that a violation of the sphericity assumption had occurred, the Greenhouse-Geisser correction was utilized. An alpha value of 0.05 was employed as the criterion for statistical significance.

3. Results

There was no significant effect of the four different face identities on discrimination thresholds ($F_{3, 15} = 2.59$; $p=0.091$). Accordingly, face discrimination thresholds were averaged across face identity and average data are considered in all subsequent analyses.

3.1. Same Viewpoint

Discrimination thresholds were measured for faces presented from a range (0° , 5° , 10° and 20°) of viewpoints (figure 3). There was no change in viewpoint between the target and comparison faces.

The frontal viewpoint condition served as a baseline to which all other conditions were compared. Data are presented as threshold elevations, relative to frontal (0°) presentation. Threshold elevations are inversely proportional to discrimination sensitivity. For instance, the mean threshold elevation for the 20° viewpoint was $1.69\times$. Therefore, a 1.69 fold increase in face distinctiveness was required to discriminate faces presented from 20° , compared to when they were presented from the frontal viewpoint.

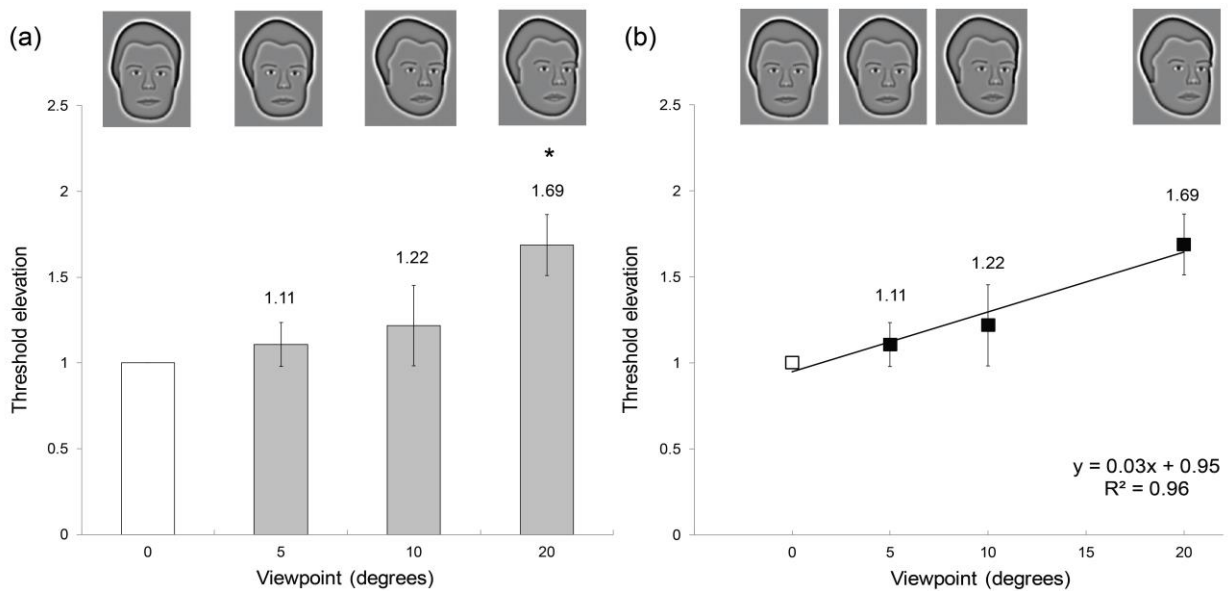


Figure 3. Same viewpoint threshold elevations. In both (a) and (b) data are expressed as threshold elevations, relative to the frontal (0°) viewpoint condition ($= 1.00$; white bar/symbol). The numbers next to each bar/symbol are mean threshold elevations. Error bars denote 95% confidence intervals throughout. The data presented in (a) suggest that face discrimination thresholds increase monotonically as faces are rotated away from the frontal (0°) viewpoint. (b) illustrates that these data support a linear relationship between viewpoint and face discrimination thresholds across the range of viewpoints that we tested. The regression equation (and associated R^2 value) describe the relationship between viewpoint and threshold

elevations. The asterisk in (a) indicates a significant increase in thresholds for face presented from the 20° side, relative to frontal, viewpoint (pairwise comparisons with Bonferroni correction; $p=0.004$). It should be noted that, although the icons depict faces rotated rightwards, each viewpoint was tested with the faces presented both to the right and left. Since there was no significant effect of direction on threshold elevations (see below), data were averaged across direction.

A two-factor (viewpoint [5°, 10°, 20°] and direction [right or left]), repeated measures ANOVA found no significant effect of direction on threshold elevation ($F_{1,5} = 0.27$; $p=0.624$; $\eta_p^2 = 0.05$). This result suggests that sensitivity is equivalent for faces rotated from the frontal viewpoint by the same magnitude in either direction.

There was a significant effect of viewpoint on threshold elevations ($F_{3,15} = 13.35$; $p<0.001$; $\eta_p^2 = 0.73$). Contrast analysis provided evidence of a linear relationship between viewpoint and threshold elevations across the range of viewpoints that we tested ($F_{1,5} = 37.66$; $p=0.002$; $\eta_p^2 = 0.88$) (figure 3b). This was supported by simple linear regression analysis ($F_{1,3} = 48.41$; $p=0.020$; $R^2=0.96$). Pairwise comparisons, with Bonferroni correction, revealed that this increase in face discrimination thresholds with rotation from the frontal viewpoint became significant at 20° ($p=0.004$). These results suggest that, within the 40° range that we tested (i.e. 20° right to 20° left), face discrimination sensitivity is highest for faces presented from the frontal (0°) viewpoint. Sensitivity progressively declines as faces are rotated away from this viewpoint in either direction, even by small amounts (e.g. 5°).

3.2. Front and side viewpoint changes

Discrimination thresholds were then measured for faces presented with a change in viewpoint. On each trial, one viewpoint was always the frontal (0°) view. In the front-to-side condition, observers were asked to match the identity of a face viewed from the front to that of faces viewed from one of three side viewpoints (5°, 10° or 20°) (figure 4a). The order was reversed for the side-to-front condition; observers matched a face presented from one of the three side viewpoints to a face viewed from the front (figure 4c).

The effects of rightward and leftward changes in face viewpoint were measured separately. A two-factor (magnitude of viewpoint change [5°, 10°, 20°] and direction [right or left]), repeated measures ANOVA found no significant effect of the direction of viewpoint change on threshold elevations ($F_{1,5} = 1.68$; $p = 0.252$, $\eta_p^2 = 0.25$). This indicates that the effects of rightward and leftward changes in viewpoint of the same magnitude are equivalent. Accordingly, threshold elevations for each viewpoint were averaged across both directions (figure 4).

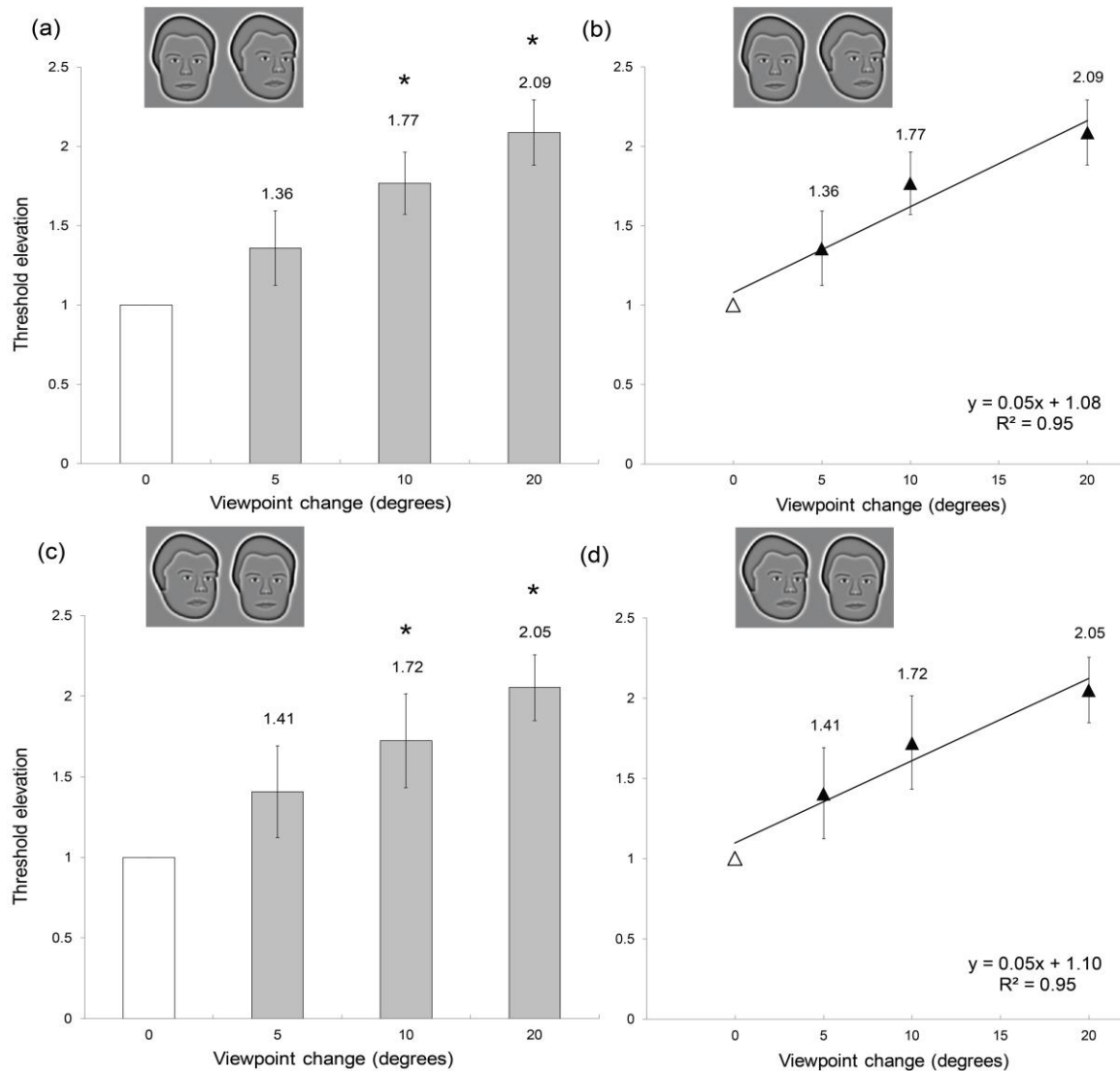


Figure 4. Front and side viewpoint changes. In (a)-(d) data are presented as threshold elevations, relative to those for the baseline condition (=1.00; white bar/symbol) in which there was no change in viewpoint. The values next to each bar are mean threshold elevations, averaged across both directions. Error bars denote 95% confidence intervals throughout. (a) Front-to-side. Observers were asked to match the identity of a target face presented from the frontal (0°) viewpoint to that of comparison faces viewed from one of three side viewpoints (5°, 10° or 20°). Icons illustrate the change in viewpoint. Asterisks indicate a significant increase in thresholds for faces presented with a 10° and 20° change in viewpoint (pairwise comparisons with Bonferroni correction; $p < 0.05$). (b) illustrates that these data support a linear relationship between the magnitude of viewpoint change and threshold elevations across the range of viewpoints that we tested. The regression equation (and associated R^2 value) describe the relationship between viewpoint change and threshold elevations. (c) + (d) present data in the same format for side-to-front viewpoint changes: observers were asked to match the identity of a target face presented from one of three side viewpoints (5°, 10° or 20°) to that of comparison faces viewed from the frontal (0°) viewpoint.

For front-to-side changes in viewpoint (figure 4a), face discrimination thresholds depended upon the magnitude of viewpoint change (one-way repeated measures ANOVA $F_{3,15} = 31.01$; $p < 0.001$; $\eta_p^2 = 0.86$). Contrast analysis provided evidence of a linear relationship between the magnitude of viewpoint change and threshold elevations across the range that we tested ($F_{1,5} = 104.14$; $p < 0.001$; $\eta_p^2 = 0.95$) (figure 4b). This was supported by simple linear regression analysis ($F_{1,3} = 38.10$; $p = 0.025$; $R^2 = 0.95$). Pairwise comparisons, with Bonferroni correction, revealed that this increase in face discrimination thresholds with changes in viewpoint became significant at 10° ($p = 0.004$) (20° ; $p = 0.001$). These results suggest that changes in viewpoint, from the frontal (0°) to side views, reduce sensitivity to face identity. Sensitivity is reduced even for small (5°) changes in viewpoint and declines linearly as the disparity in viewpoint is increased. Based on the simple linear regression, we estimate that each 5° of viewpoint change reduces sensitivity to face identity is reduced by a factor of 1.18.

The same pattern of results was identified for side-to-front changes in viewpoint (figure 4c). Specifically, face discrimination thresholds depended upon the magnitude of viewpoint change (one-way repeated measures ANOVA $F_{3,15} = 18.68$; $p < 0.001$; $\eta_p^2 = 0.79$) and there was evidence of a linear relationship ($F_{1,5} = 113.42$; $p < 0.001$; $\eta_p^2 = 0.96$) (figure 4d). This was supported by simple linear regression analysis ($F_{1,3} = 39.35$; $p = 0.024$; $R^2 = 0.95$). Pairwise comparisons, with Bonferroni correction, revealed that this increase in face discrimination thresholds with changes in viewpoint became significant at 10° ($p = 0.027$) (20° ; $p = 0.001$). These results suggest that changes in viewpoint, from side views to the frontal (0°) viewpoint, reduce sensitivity to face identity. Sensitivity was impaired by small (5°) changes in viewpoint and progressively declined as the magnitude of viewpoint change was increased.

We found no difference in the effect of front-to-side and side-to-front changes in viewpoint on sensitivity to face identity ($F_{1,5} = 0.01$; $p = 0.934$; $\eta_p^2 < 0.01$). This indicates that the effect of rotations in viewing angle either from (front-to-side) or towards (side-to-front) the frontal viewpoint are equivalent. Further, the slopes of the regression equations in figure 4 suggest a comparable reduction in sensitivity to face identity with changes in face viewpoint in either direction.

Our results suggest that changes in viewpoint significantly impair sensitivity to face identity. This reduction in sensitivity, however, is relative to that for faces viewed from the frontal viewpoint. Importantly, our data also indicate that there are considerable differences in sensitivity to faces presented from different viewpoints (figure 3). Specifically, when viewpoint was fixed (same viewpoint condition, see section 3.1), sensitivity was significantly higher for faces presented from the frontal, compared to a side, viewpoints. Consequently, the reduced

sensitivity associated with changes in viewpoint from 0-20° (or vice versa) could be explained by reduced sensitivity to faces presented from side (20°) viewpoints.

In order to create a level playing field, we compared discrimination thresholds for each magnitude of viewpoint change to those for the associated same viewpoint condition (e.g. thresholds for the 20° viewpoint change condition were compared to those for the same viewpoint condition when all face were presented from 20°) (figure 5).

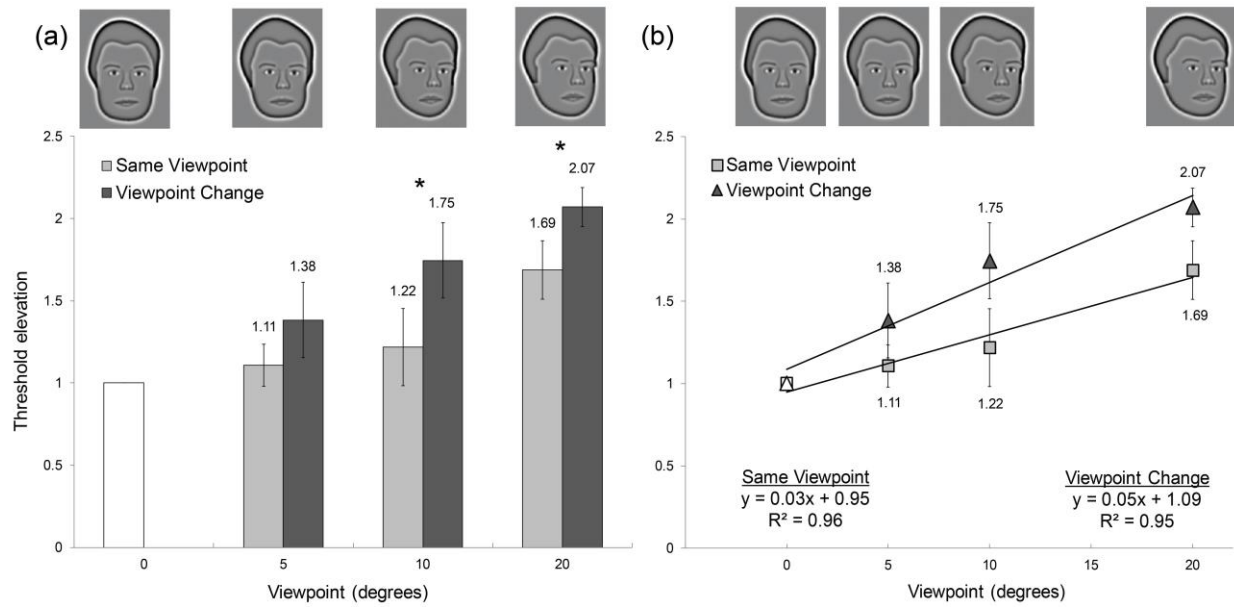


Figure 5. The effect of changes in viewpoint on face discrimination thresholds. In both (a) and (b) data are expressed as threshold elevations, relative to the frontal (0°) baseline (= 1.00; white bar/symbol). The numbers next to each bar/symbol are mean threshold elevations. Error bars denote 95% confidence intervals. Light gray bars/symbols represent threshold elevations for faces presented with no change in viewpoint (figure 3). Dark bars/symbols represent threshold elevations for faces presented with a change in viewpoint (figure 4). These values were calculated by averaging threshold elevations for front-to-side and side-to-front changes in viewpoints. The difference in the heights of the bars in (a) illustrates the effect of viewpoint change, when differences in baseline sensitivity to faces presented from front and side viewpoints has been taken into account. This is supported by the separation of the regression lines in (b). The regression equations (and associated R^2 values) describe the relationship between viewpoint and threshold elevations. Asterisks in (a) denote a significant increase in thresholds with a change in viewpoint, relative to the associated same viewpoint baseline (pairwise comparisons; $p < 0.05$).

A two-factor (magnitude of viewpoint change [5°, 10°, 20°] and viewpoint change [same viewpoint or changed viewpoint]), repeated measures ANOVA found a significant effect of viewpoint change on threshold elevations ($F_{1,5} = 22.47$; $p = 0.005$; $\eta_p^2 = 0.82$). This result indicates that changes in viewpoint significantly increase discrimination thresholds, even when differences in baseline sensitivity (i.e. no change in viewpoint) to front and side viewpoints are taken into account.

One-tailed t -tests (with Holm-Bonferroni correction) revealed that discrimination thresholds were significantly increased by a change in viewpoint, relative to the same viewpoint condition, at 10° ($t(5) = 5.24$; $p=0.002$) and 20° ($t(5) = 2.72$; $p=0.021$).

In sum, changes in face viewpoint significantly increased face discrimination thresholds. Thresholds for identifying faces across a change in viewpoint were significantly higher than those for the viewpoint associated with poorest sensitivity. Accordingly, the increase in thresholds associated with viewpoint changes cannot be explained by reduced sensitivity to faces presented from side viewpoints. These results indicate that changes in viewpoint reduce sensitivity to face identity, even when differences in baseline sensitivity to different viewpoints are taken into account.

3.3. Symmetrical Viewpoint Changes

In this condition, observers were required to match the identity of faces across changes in viewpoint which were symmetrical (i.e. equal in magnitude) around the frontal axis. For example, a 40° symmetrical viewpoint change required observers to match the identity of a target face presented from 20° right side view with that of comparison faces shown from a 20° left side view.

As previously, there was no significant effect of direction (right or left) on threshold elevations ($F_{1,5} = 0.85$; $p=0.399$; $\eta_p^2 = 0.15$). Accordingly, threshold elevations for each magnitude of viewpoint change were averaged across both directions (figure 6).

There was a significant effect of the magnitude of viewpoint change on threshold elevations ($F_{3,15} = 14.46$; $p<0.001$; $\eta_p^2 = 0.74$) (figure 6a). Contrast analysis provided evidence of a linear relationship between the magnitude of viewpoint change and threshold elevations across the range that we tested ($F_{1,5} = 36.30$; $p=0.002$; $\eta_p^2 = 0.88$) (figure 6b). This was supported by simple linear regression analysis ($F_{1,3} = 259.12$; $p=0.004$; $R^2=0.99$). Pairwise comparisons, with Bonferroni correction, revealed that this increase in face discrimination thresholds became significant at 40° ($p=0.004$) changes in viewpoint.

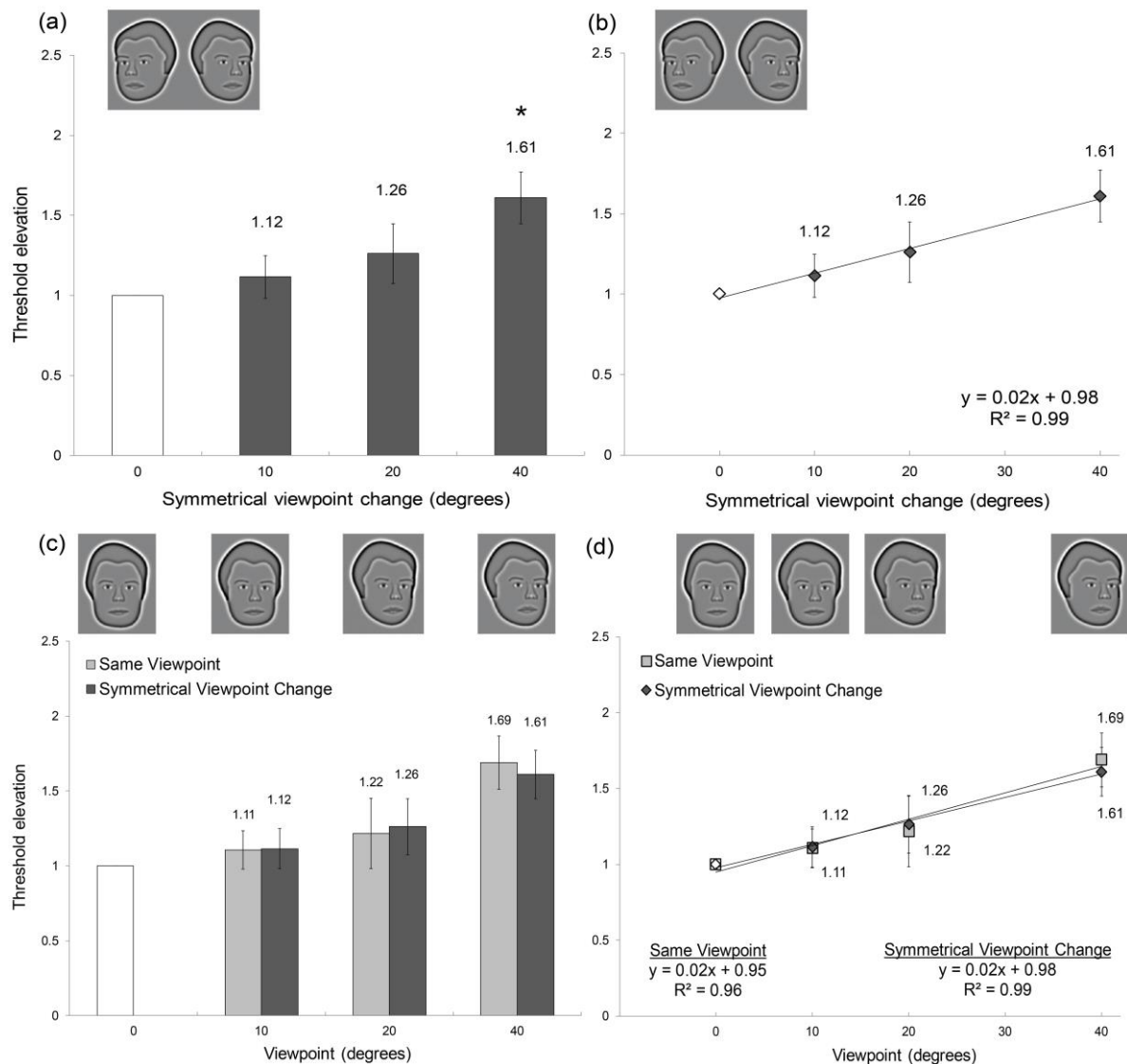


Figure 6. Symmetrical changes in viewpoint. In (a)-(d) data are presented as threshold elevations, relative to those for the baseline condition (=1.00; white bar/symbol) in which there was no change in viewpoint. The values next to each bar are mean threshold elevations, averaged across both directions (right and left). Error bars denote 95% confidence intervals throughout. (a) Observers were asked to match face identity across changes in viewpoint which were symmetrical around the frontal axis. Icons illustrate an example change in viewpoint. Asterisk indicates a significant increase in thresholds for faces presented with a 40° change in viewpoint (pairwise comparisons with Bonferroni correction; $p=0.004$). (b) illustrates that these data support a linear relationship between the magnitude of viewpoint change and threshold elevations across the range of viewpoints that we tested. The regression equation describes the relationship between viewpoint change and threshold elevations. (c) and (d) compare threshold elevations from (a) (dark bars/symbols) with those for the condition in which there was no change in viewpoint (light gray bars- figure 3). For example, the mean threshold

elevation associated with a symmetrical viewpoint change of 40° (20° right to 20° left: 1.61) was compared to that for the 20° same viewpoint condition (1.69) (figure 3). The heights of the bars for each viewpoint in (c) appear comparable. This suggests that symmetrical changes in viewpoint do not increase thresholds beyond what would be expected based on sensitivity to the component viewpoints (e.g. 20° side). This is supported by the overlap in the regression lines for the same viewpoint and symmetrical viewpoint change conditions in (d).

These data suggest that symmetrical changes in face viewpoint reduce sensitivity to face identity. Sensitivity declines gradually as the magnitude of the symmetrical change in viewpoint is increased (figure 6b). As outlined above, however, thresholds are expressed relative to those for faces viewed from the frontal viewpoint. The same viewpoint condition (see section 3.1) demonstrated that sensitivity is significantly poorer for faces viewed from the 20° side, relative to frontal, viewpoint. Accordingly, the reduction in sensitivity with large symmetrical viewpoint changes may be explained by differences in baseline sensitivity to front and side viewpoints.

Discrimination thresholds for each magnitude of symmetrical viewpoint change were compared to those for the associated same viewpoint condition (figure 6c). For example, thresholds for the 40° symmetrical viewpoint change were compared to those for the 20° side same viewpoint condition.

A two-factor (magnitude of viewpoint change [5°, 10°, 20°] and viewpoint change [same viewpoint or changed viewpoint]), repeated measures ANOVA found no significant effect of viewpoint change on threshold elevations ($F_{1,5} = 0.05$; $p=0.830$; $\eta_p^2 = 0.01$).

This result demonstrates that the increase in thresholds identified for the 40° symmetrical viewpoint change condition can be explained by elevated thresholds for faces presented from the 20° side, relative to frontal, viewpoint. The symmetrical viewpoint change does not increase thresholds further than would be expected based on sensitivity to the component viewpoints (i.e. 20° side right and left).

In sum, symmetrical changes in viewpoint do not impair the ability to discriminate between face identities. This is in sharp contrast to the effects of both front-side and side-front viewpoint changes outlined above.

4. General Discussion

The present study quantified the effect of variations in viewpoint on the ability to discriminate between different face identities. When viewpoint was fixed, face discrimination ability varied significantly with the viewpoint from which faces were presented. We found that sensitivity declines linearly as faces were rotated away from the frontal viewpoint. Specifically, sensitivity to faces presented from 20° side views was 1.69 times poorer than that for faces presented from the frontal viewpoint. Introducing changes in viewpoint led to further reductions in discrimination ability. Face discrimination sensitivity declined monotonically as the magnitude of viewpoint change was increased. Further, when the magnitude was fixed, the decline in sensitivity was not equivalent for different types of viewpoint change. For example, relative to the same viewpoint baseline, a 20° rotation from the frontal-to-side viewpoint reduced face discrimination sensitivity by a factor of 2.07. A 20° rotation which was symmetrical around the frontal axis (i.e. 10° right to 10° left), however, had no significant effect on discrimination sensitivity (threshold elevation = 1.26). These results indicate that the reduction in sensitivity associated with changes in viewpoint is determined by other factors, such as symmetry, in addition to the magnitude of viewpoint change.

4.1. Same viewpoint

A key finding of the present study is that the ability to discriminate between face identities depends upon viewpoint. When viewpoint was fixed (same viewpoint condition), across the range of viewpoints that we tested (20° right to 20° left), sensitivity was highest for faces presented from the frontal viewpoint. Face discrimination sensitivity declined monotonically as the face viewing angle was rotated away from the frontal viewpoint, in either direction (i.e. left or right), even by small amounts (e.g. 5°). Specifically, our data support a linear relationship between viewpoint and face discrimination sensitivity. This decline in face discrimination sensitivity, relative to that measured at the frontal viewpoint, reached significance when faces were presented at 20 degrees. This viewpoint-dependency in an unfamiliar face discrimination task is consistent with previous studies. Specifically, it has been reported that sensitivity is significantly higher for faces presented from frontal, relative to side, viewpoints (Habak et al., 2008; Lee et al., 2006; Wilson et al., 2002). For example, Van der Linde and Watson (2010) found that performance on a same/different identity discrimination task was best when faces were presented from the frontal viewpoint and significantly poorer when the faces were shown from a 30° viewing angle. Our data are consistent with this premise, but extend the result to smaller viewing angles. Specifically, we found that face discrimination sensitivity declined as faces were rotated from the frontal viewpoint by 5 degrees. When combined with previous studies, our data suggest that the reduced sensitivity to faces reported with larger viewing angles (20° or more) is a continuation of the decline identified with smaller viewing angles (e.g.

5°). Our results indicate that even modest variations in the angle from which faces are viewed influence the ability to discriminate between face identities.

It has been proposed that this frontal-view advantage can be explained by bilateral symmetry of the face (Lee et al., 2006). Owing to natural variations in feature position and size, faces are not perfectly symmetrical from any viewpoint. Nevertheless, the frontal viewpoint gives rise to a significantly greater degree of symmetry than side views. Visual discrimination of complex objects which are highly symmetrical is significantly more efficient than that for asymmetrical objects (Barlow & Reeves, 1979; Z. Liu & Kersten, 2003; Wilson, Wilkinson, Lin et al., 2000). These results have been interpreted as evidence that, through introducing significant information redundancy, symmetry enhances the efficiency of visual processing. Specifically for faces, symmetry between the right and left face halves enables identity discrimination judgements to be made based on one half of the face only (Lee et al., 2006). This is consistent with our finding that sensitivity is highest to faces presented from the viewpoint which gives rise to the highest degree of symmetry.

On the other hand, a recent study found no advantage for symmetrical, relative to asymmetrical, faces on an identity discrimination task (Bittner & Gold, 2017). This may be explained by the observation that even small (5°) rotations of viewpoint introduce a considerably greater degree of asymmetry between the left and right halves of the face than that found in the frontal face images employed by Bittner and Gold. Further, Bittner and Gold's approach measured the minimum contrast energy required for reliable discrimination of face identity. The extent to which discriminating between face images presented at very low contrast investigates typical face processing remains unclear.

Our data could be interpreted as suggesting that the frontal viewpoint is optimal for unfamiliar face discrimination, and sensitivity declines monotonically with angular rotation in either direction. Importantly, however, the present study focused upon a small range of angular rotations ($\pm 20^\circ$), centered upon the frontal view. This ensured that the individual features of faces presented from the side were partially, rather than completely, obscured (Guy et al., 2017; Morin et al., 2015). In order to extrapolate our data to faces presented from larger viewing angles, one would need to assume that the relationship between viewing angle and face discrimination sensitivity remains linear beyond the range that we tested. There is evidence to suggest that this is not a valid assumption. For example, previous reports suggest that the three-quarter (45°) viewpoint may offer a comparable advantage to that of the frontal viewpoint for identification of unfamiliar faces (Bruce et al., 1987; Nordt & Weigelt, 2017; O'toole et al., 1998). The evidence for the three-quarter advantage is, however, mixed (Hill et al., 1997; C. H. Liu & Chaudhuri, 2002). To resolve this ambiguity, future work could

systematically measure face discrimination thresholds at viewpoints ranging from frontal to profile (90°).

4.2. Changes in viewpoint

The present study demonstrated that changes in face viewpoint impair the ability to discriminate between face identities. Our study focused upon small (up to 20°) changes in viewpoint, centered upon the frontal view. Our data point to a linear decline in sensitivity to face identity as the magnitude of viewpoint change is increased. This continuous decline highlighted that even 5° variations in viewpoint were sufficient to impair face discrimination ability. For example, relative to that for faces presented from the same (frontal) viewpoint, introducing a 5° disparity in viewpoint reduced discrimination sensitivity by a factor of 1.38. A 20° rotation, on the other hand, reduced sensitivity by a factor of 2.07. Based on a regression analysis, we estimate that, on average, sensitivity to face identity is reduced by a factor of 1.18 for each additional five degrees of viewpoint change. These findings are not specific to rotation away from the frontal viewpoint; we found equivalent costs of viewpoint change for faces rotated from side views to frontal presentation.

As outlined above, when viewpoint was fixed, there was a linear decline in face discrimination sensitivity as the face viewing angle was rotated away from the frontal viewpoint. For example, discrimination threshold for faces viewed from a 20° side view were significantly higher than those presented from the frontal viewpoint. The cost of viewpoint change, however, was determined relative to discrimination sensitivity for faces presented from the frontal viewpoint. Accordingly, the increase in discrimination thresholds associated with a change in viewpoint from 0-20° could be explained by reduced sensitivity to faces presented from the 20° side view. Our data, however, show that thresholds for a 0-20° viewpoint change were significantly higher than those for the 20° side same viewpoint condition. This additional threshold elevation demonstrates that changes in viewpoint reduce sensitivity beyond that which would be predicted based on the viewpoint associated with poorest baseline performance.

These results support the proposal that modest changes in face viewpoint, anchored around the frontal view, impair face discrimination ability (Favelle et al., 2011; Habak et al., 2008; Lee et al., 2006; Van der Linde & Watson, 2010). Data from the present study extend this premise by suggesting that this impairment is related to a continuous decline in face discrimination sensitivity with increasing magnitude of viewpoint change. Sensitivity is greatest with no changes in viewpoint; even small (5°) variations in viewpoint are sufficient to impair sensitivity.

Our results indicate that the effect of viewpoint changes on sensitivity to face identity is independent of the viewpoint from which faces are originally shown or the viewpoint from which the discrimination judgments has to be made. For example, discrimination thresholds for faces

presented with either a front-to-side (e.g. 0° to 20° right) or side-to-front (e.g. 20° right to 0°) viewpoint change were equivalent. This finding is in line with previous reports (Favelle et al. 2011; Valentin, Abdi & Edelman, 1999). Participants in these studies judged if two face images depicted the same person, or two different identities. The results indicated that, whilst performance depended upon the change in viewpoint between the two faces, there was minimal effect of the viewpoint of the first (or encoding) face. These findings are in agreement with those of the present study: sensitivity to face identity is (partly) determined by the magnitude of the viewpoint change, but not the order in which the viewpoints are presented. Troje and Bühlhoff (1996), on the other hand, found that identity discrimination accuracy depended on the viewpoint from which the initial (i.e. 'learning') face was presented. Specifically, presenting learning faces from viewing angles of 20-70° improved performance, relative to when learning faces were presented from near frontal or profile views. Since the maximum viewing angle tested by the present study was 20°, it remains possible that an effect of the viewpoint from which the learning (i.e. target) face was presented would have emerged at larger viewing angles, and this possibility could be tested in future work.

The results of the present study point to the conclusion that encoding of unfamiliar face identities is viewpoint-dependent. This is in agreement with findings from electrophysiological studies of face-selective neurons within the temporal cortex of the macaque monkey (Perrett et al., 1991). Activity of the majority of these cells is maximal for a specific viewpoint, and declines as face viewing angle is rotated in either direction. Similarly, in humans, viewpoint is a major determinant of neural activity within brain areas which have been implicated in face processing (Weibert, Flack, Young et al., 2018). fMRI adaptation studies indicate that different viewpoints of unfamiliar faces are encoded by dissociable populations of neurons within the FFA (Andrews & Ewbank, 2004; Ewbank & Andrews, 2008; Xu et al., 2009). For example, a 4° change in face viewing angle was sufficient to release the fMRI BOLD signal from the adaptation associated with repeated viewing of the same face identity (Ewbank & Andrews, 2008). Similarly, the amplitude of the M170 demonstrates selectivity for small changes (e.g. 2°) in face viewpoint (Ewbank, Smith, Hancock & Andrews, 2007). This suggests narrow tuning of face-selective regions for viewpoint and is consistent with data from the present study. Specifically, we found evidence of a decline in sensitivity to face identity with changes in viewpoint which could be detected at small (5°) viewing angles.

In line with the premise of dissociable encoding of different face viewpoints, following adaptation to a face presented from a side view, a subsequently-viewed test face, shown from the frontal (0°) viewpoint, appears rotated in the opposite direction (Chen, Yang, Wang et al., 2010; Daar & Wilson, 2012; Fang & He, 2005). This repulsive aftereffect suggests that different viewpoints are encoded by the activity of discrete channels of neurons, which can be independently influenced by adaptation. Increasing the difference in viewpoint between the

adapting and test faces significantly diminishes the viewpoint aftereffect (Fang & He, 2005). This further suggests that different viewpoints are encoded by dissociable channels of neurons: adapting to one viewpoint has minimal effect on sensitivity to other viewpoints which are represented by different neuronal populations. In line with this premise, face distortion and identity aftereffects transfer poorly across viewpoint (Jeffery, Rhodes & Busey, 2006; Jiang, Blanz & O'Toole, 2006).

4.3. Symmetrical changes in viewpoint

Previous reports point to the conclusion that the cost of viewpoint changes on face discrimination ability depends upon the magnitude of change in face viewing angle. This is consistent with our data which provided evidence of a linear decline in face discrimination sensitivity with increasing magnitude of viewpoint change. The present study, however, further revealed that the reduction in discrimination sensitivity depends upon factors other than magnitude. As outlined above, introducing changes in viewpoint significantly reduced sensitivity to faces presented from the frontal viewpoint. On the other hand, viewpoint changes which were symmetrical around the frontal axis had no significant effect on face discrimination sensitivity. When differences in baseline sensitivity to front and side face viewing angles were taken into account, face discrimination ability was even robust to large (40°) symmetrical viewpoint changes.

Our data support the premise that face identification ability is robust to symmetrical changes in viewing angle (Bruce et al., 1987; Hill et al., 1997; C. H. Liu & Chaudhuri, 2002; Schyns & Bülthoff, 1994; Troje & Bülthoff, 1998; Van der Linde & Watson, 2010). While previous reports focused upon large changes in viewing angle (e.g. 90°: 45° right to 45° left), the present study has extended evidence for this symmetrical viewpoint advantage to considerably smaller variations in viewing angle (10-40°) from the frontal viewpoint. Further, our data have provided evidence of a robust symmetrical viewpoint advantage on an unfamiliar face discrimination task, without a memory requirement. This suggests that the origin of the ability to match identities across symmetrical changes in viewpoint is perceptual, rather than based within memory.

This behavioral evidence is in line with electrophysiological reports which have identified populations of face-selective neurons which demonstrate a bimodal tuning pattern for viewpoint (Freiwald & Tsao, 2010; Logothetis & Sheinberg, 1996; Perrett et al., 1991). Specifically, these reports have identified cells within temporal cortex of the macaque monkey which respond strongly to a particular viewpoint and its symmetrical counterpoint, but not intervening viewpoints.

4.4. Limitations

One limitation of the present study is that the faces were presented as static images. Changes in face viewpoint, however, typically include dynamic changes over time. It has been proposed that this information could facilitate face identification across viewpoint changes (Lander & Bruce, 2000). Previous reports have identified an advantage of facial motion for familiar face recognition (Lander & Bruce, 2003; Pike, Kemp, Towell et al., 1997). Current evidence, however, indicates that replacing static images with dynamic sequences does not aid unfamiliar face discrimination across viewpoints (Christie & Bruce, 1998; Lee, Habak & Wilson, 2010). These results support the premise that encoding of unfamiliar faces is viewpoint-dependent.

A further limitation is that, in line with the majority of face perception studies, we employed two-dimensional face images as stimuli. Real faces, however, feature three-dimensional information, which varies with changes in viewpoint. Accordingly, information was excluded which may be utilized by the visual system to discriminate between real face identities. Evidence of an advantage for three-dimensional faces on a cross-viewpoint identification task is mixed. While some reports suggest that identification accuracy is higher with three-dimensional, relative to two-dimensional faces (Burke, Taubert & Higman, 2007; Chelnokova & Laeng, 2011), others found no difference (Hong Liu, Ward & Young, 2006).

Our results suggest that representations of unfamiliar faces are viewpoint-dependent. The effects of viewpoint change on perceptual sensitivity may be different for familiar faces, which may be represented in a qualitatively different way (Troje & Bülthoff, 1998). Specifically, behavioral evidence suggests that recognition accuracy for familiar faces is more robust to changes in viewpoint than that for unfamiliar faces. Further, neuroimaging studies indicate that representations of familiar, relative to unfamiliar, faces within the FFA are more tolerant to variations in viewpoint (Ewbank & Andrews, 2008). This is consistent with the view that, while representations of unfamiliar faces are initially image-based, familiarity leads to the development of structural face representations which enable recognition of identity across changes in viewing conditions (e.g. facial expression, lighting and viewpoint) (Bruce & Young, 1986).

Synthetic faces are simplified stimuli which do not feature all of the information available from a real face. Do the results presented here for synthetic faces generalize to everyday face perception? Although they are simplified, substantial evidence points to the conclusion that synthetic faces are processed in the same way as face photographs. For example, synthetic faces retain sufficient identifying information to permit recognition at the individual level, even across changes in viewpoint (Wilson et al., 2002). Neuroimaging evidence indicate that synthetic faces and face photographs elicit a comparable BOLD signal in the FFA (Loffler, Yourganov, Wilkinson et al., 2005). Synthetic faces demonstrate classic behavioral hallmark of

face processing, such as the face inversion effect (Logan, Wilkinson, Wilson et al., 2016; Wilson et al., 2002), left-over-right visual field bias (Schmidtman, Logan, Kennedy et al., 2015) and external feature advantage for unfamiliar face discrimination (Logan, Gordon & Loffler, 2017). Finally, patients with developmental prosopagnosia demonstrate a significant impairment with face photographs and synthetic faces, but not other objects, such as cars (Lee et al., 2010; Logan et al., 2016).

5. Conclusions

The present study employed a novel metric to quantify the effect of variations in viewpoint on the ability to discriminate between unfamiliar face identities. Our data indicate that, within the 20° right to 20° left range that we tested, sensitivity to face identity is greatest for faces presented from the frontal viewpoint. Sensitivity declined linearly as faces were rotated away from this frontal viewpoint, even by small amounts (5°). This decline in sensitivity reached significance when faces were rotated to 20°. Changes in viewpoint further impair face discrimination ability: sensitivity declined linearly as the magnitude of the viewpoint change was increased. We estimated that each 5° of viewpoint change reduces sensitivity to face identity is reduced by a factor of 1.18. Importantly, however, face identity discrimination is robust to substantial changes in viewpoint which are symmetrical around the frontal axis. These results suggest that encoding of unfamiliar face identities is viewpoint-dependent, and that symmetry may be utilized by the visual system in order to recognize faces across changes in viewpoint.

6. Acknowledgements

The authors are grateful to Dr James Heron and Prof Gunter Loffler for useful discussions on the interpretation of our data. We also thank anonymous reviewers for their helpful comments on an earlier draft of this manuscript.

Declarations of interest: none

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

7. References

- Andrews, T. J., & Ewbank, M. P. (2004). Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *NeuroImage*, 23, 905-913.
- Axelrod, V., & Yovel, G. (2012). Hierarchical processing of face viewpoint in human visual cortex. *Journal of Neuroscience*, 32, 2442-2452.
- Barlow, H. B., & Reeves, B. C. (1979). The versatility and absolute efficiency of detecting mirror symmetry in random dot displays. *Vision Research*, 19, 783-793.

- Bittner, J. L., & Gold, J. M. (2017). The impact of symmetry on the efficiency of human face perception. *Perception*, 46, 830-859.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433-436.
- Bruce, V. (1982). Changing faces: Visual and non-visual coding processes in face recognition. *British Journal of Psychology*, 73, 105-116.
- Bruce, V., Valentine, T., & Baddeley, A. (1987). The basis of the 3/4 view advantage in face recognition. *Applied Cognitive Psychology*, 1, 109-120.
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, 77, 305-327.
- Burke, D., Taubert, J., & Higman, T. (2007). Are face representations viewpoint dependent? A stereo advantage for generalising across different views of faces. *Vision Research*, 47, 2164-2169.
- Chelnokova, O., & Laeng, B. (2011). Three-dimensional information in face recognition: An eye-tracking study. *Journal of Vision*, 11, 27.
- Chen, J., Yang, H., Wang, A., & Fang, F. (2010). Perceptual consequences of face viewpoint adaptation: Face viewpoint aftereffect, changes of differential sensitivity to face view, and their relationship. *Journal of Vision*, 10, 12.
- Christie, F., & Bruce, V. (1998). The role of dynamic information in the recognition of unfamiliar faces. *Memory & Cognition*, 26, 780-790.
- Daar, M., & Wilson, H. R. (2012). The face viewpoint aftereffect: Adapting to full faces, head outlines, and features. *Vision Research*, 53, 54-59.
- De Souza, W. C., Eifuku, S., Tamura, R., Nishijo, H., & Ono, T. (2005). Differential characteristics of face neuron responses within the anterior superior temporal sulcus of macaques. *Journal of Neurophysiology*, 94(2), 1252-1266.
- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, 4, 2051-2062.
- Ewbank, M. P., Smith, W. A., Hancock, E. R., & Andrews, T. J. (2007). The M170 reflects a viewpoint-dependent representation for both familiar and unfamiliar faces. *Cerebral Cortex*, 18(2), 364-370.
- Ewbank, M. P., & Andrews, T. J. (2008). Differential sensitivity for viewpoint between familiar and unfamiliar faces in human visual cortex. *NeuroImage*, 40, 1857-1870.
- Fang, F., & He, S. (2005). Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. *Neuron*, 45, 793-800.
- Favelle, S. K., Palmisano, S., & Avery, G. (2011). Face viewpoint effects about three axes: The role of configural and featural processing. *Perception*, 40(7), 761-784.
- Favelle, S., Hill, H., & Claes, P. (2017). About face: Matching unfamiliar faces across rotations of view and lighting. *i-Perception*, 8, 2041669517744221.

- Freiwald, W. A., & Tsao, D. Y. (2010). Functional compartmentalization and viewpoint generalization within the macaque face-processing system. *Science*, 330, 845-851.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, 24, 187-203.
- Guy, J., Habak, C., Wilson, H. R., Mottron, L., & Bertone, A. (2017). Face perception develops similarly across viewpoint in children and adolescents with and without autism spectrum disorder. *Journal of Vision*, 17, 38.
- Habak, C., Wilkinson, F., & Wilson, H. R. (2008). Aging disrupts the neural transformations that link facial identity across views. *Vision Research*, 48, 9-15.
- Hill, H., Schyns, P. G., & Akamatsu, S. (1997). Information and viewpoint dependence in face recognition. *Cognition*, 62, 201-222.
- Hong Liu, C., Ward, J., & Young, A. W. (2006). Transfer between two-and three-dimensional representations of faces. *Visual Cognition*, 13, 51-64.
- Jeffery, L., Rhodes, G., & Busey, T. (2006). View-specific coding of face shape. *Psychological Science*, 17, 501-505.
- Jiang, F., Blanz, V., & O'Toole, A. J. (2006). Probing the visual representation of faces with adaptation: A view from the other side of the mean. *Psychological Science*, 17, 493-500.
- Kietzmann, T. C., Gert, A. L., Tong, F., & König, P. (2017). Representational dynamics of facial viewpoint encoding. *Journal of Cognitive Neuroscience*, 29, 637-651.
- Kietzmann, T. C., Swisher, J. D., König, P., & Tong, F. (2012). Prevalence of selectivity for mirror-symmetric views of faces in the ventral and dorsal visual pathways. *Journal of Neuroscience*, 32, 11763-11772.
- Kleiner, M., Brainard, D., Pelli, D. (2007). What's new in psychtoolbox-3. *Perception*, 36, ECVF Abstract Supplement.
- Lander, K., & Bruce, V. (2003). The role of motion in learning new faces. *Visual Cognition*, 10, 897-912.
- Lander, K., & Bruce, V. (2000). Recognizing famous faces: Exploring the benefits of facial motion. *Ecological Psychology*, 12, 259-272.
- Lander, K., & Butcher, N. (2015). Independence of face identity and expression processing: exploring the role of motion. *Frontiers in psychology*, 6, 255.
- Lee, Y., Habak, C., & Wilson, H. R. (2010). Seeing an unfamiliar face in rotational motion does not aid identity discrimination across viewpoints. *Vision Research*, 50, 854-859.
- Lee, Y., Matsumiya, K., & Wilson, H. R. (2006). Size-invariant but viewpoint-dependent representation of faces. *Vision Research*, 46, 1901-1910.
- Liu, C. H., & Chaudhuri, A. (2002). Reassessing the 3/4 view effect in face recognition. *Cognition*, 83, 31-48.

- Liu, Z., & Kersten, D. (2003). Three-dimensional symmetric shapes are discriminated more efficiently than asymmetric ones. *Journal of the Optical Society of America A*, 20, 1331-1340.
- Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience*, 8, 1386.
- Logan, A. J., Gordon, G. E., & Loffler, G. (2017). Contributions of individual face features to face discrimination. *Vision Research*, 137, 29-39.
- Logan, A. J., Wilkinson, F., Wilson, H. R., Gordon, G. E., & Loffler, G. (2016). The Caledonian face test: A new test of face discrimination. *Vision Research*, 119, 29-41.
- Logothetis, N. K., & Sheinberg, D. L. (1996). Visual object recognition. *Annual Review of Neuroscience*, 19, 577-621.
- McKone, E. (2008). Configural processing and face viewpoint. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 310.
- Meinhardt-Injac, B., Meinhardt, G., & Schwaninger, A. (2009). Does matching of internal and external facial features depend on orientation and viewpoint? *Acta Psychologica*, 132, 267-278.
- Morin, K., Guy, J., Habak, C., Wilson, H. R., Pagani, L., Mottron, L., & Bertone, A. (2015). Atypical face perception in autism: A point of view? *Autism Research*, 8, 497-506.
- Näsänen, R. (1999). Spatial frequency bandwidth used in the recognition of facial images. *Vision Research*, 39, 3824-3833.
- Newell, F. N., Chiroro, P., & Valentine, T. (1999). Recognizing unfamiliar faces: The effects of distinctiveness and view. *The Quarterly Journal of Experimental Psychology: Section A*, 52, 509-534.
- Nordt, M., & Weigelt, S. (2017). Face recognition is similarly affected by viewpoint in school-aged children and adults. *PeerJ*, 5, e3253.
- O'toole, A. J., Edelman, S., & Bülthoff, H. H. (1998). Stimulus-specific effects in face recognition over changes in viewpoint. *Vision Research*, 38, 2351-2363.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437-442.
- Perrett, D. I., Oram, M. W., Harries, M. H., Bevan, R., Hietanen, J. K., Benson, P. J., & Thomas, S. (1991). Viewer-centred and object-centred coding of heads in the macaque temporal cortex. *Experimental Brain Research*, 86, 159-173.
- Perrett, D. I., Mistlin, A. J., & Chitty, A. J. (1987). Visual neurones responsive to faces. *Trends in Neurosciences*, 10, 358-364.
- Perrett, D. I., Smith, P., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., & Jeeves, M. A. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 223, 293-317.

- Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 335, 23-30.
- Pike, G. E., Kemp, R. I., Towell, N. A., & Phillips, K. C. (1997). Recognizing moving faces: The relative contribution of motion and perspective view information. *Visual Cognition*, 4, 409-438.
- Quick, R. F. (1974). A vector-magnitude model of contrast detection. *Kybernetik*, 16, 65-67.
- Ramírez, F. M. (2018). Orientation encoding and viewpoint invariance in face recognition: Inferring neural properties from large-scale signals. *The Neuroscientist*, 24, 582-608.
- Schmidtman, G., Logan, A. J., Kennedy, G. J., Gordon, G. E., & Loffler, G. (2015). Distinct lower visual field preference for object shape. *Journal of Vision*, 15, 18.
- Schwaninger, A., & Yang, J. (2011). The application of 3D representations in face recognition. *Vision Research*, 51(9), 969-977.
- Schweinberger, S. R., & Soukup, G. R. (1998). Asymmetric relationships among perceptions of facial identity, emotion, and facial speech. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1748.
- Schyns, P. G., & Bülthoff, H. H. (1994). Viewpoint dependence and face recognition. In *Proceedings of the XVI meeting of the Cognitive Science Society* (pp. 789-793). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Tanaka, K., Saito, H., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology*, 66, 170-189.
- Troje, N. F., & Bülthoff, H. H. (1998). How is bilateral symmetry of human faces used for recognition of novel views? *Vision Research*, 38, 79-89.
- Troje, N. F., & Bülthoff, H. H. (1996). Face recognition under varying poses: The role of texture and shape. *Vision Research*, 36, 1761-1771.
- Valentin, D., Abdi, H., & Edelman, B. (1999). From rotation to disfiguration: Testing a dual-strategy model for recognition of faces across view angles. *Perception*, 28(7), 817-824.
- Van der Linde, I., & Watson, T. (2010). A combinatorial study of pose effects in unfamiliar face recognition. *Vision research*, 50(5), 522-533.
- Weibert, K., Flack, T. R., Young, A. W., & Andrews, T. J. (2018). Patterns of neural response in face regions are predicted by low-level image properties. *Cortex*, 103, 199-210.
- Wilkinson, F., Wilson, H. R., & Habak, C. (1998). Detection and recognition of radial frequency patterns. *Vision Research*, 38, 3555-3568.
- Wilson, H. R., Loffler, G., & Wilkinson, F. (2002). Synthetic faces, face cubes, and the geometry of face space. *Vision Research*, 42, 2909-2923.
- Wilson, H. R., & Wilkinson, F. (2002). Symmetry perception: A novel approach for biological shapes. *Vision Research*, 42, 589-597.

- Wilson, H. R., Wilkinson, F., Lin, L., & Castillo, M. (2000). Perception of head orientation. *Vision Research*, 40, 459-472.
- Xu, X., Yue, X., Lescroart, M. D., Biederman, I., & Kim, J. G. (2009). Adaptation in the fusiform face area (FFA): Image or person? *Vision Research*, 49, 2800-2807.